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Study scale determines whether wildlife loss protects against or promotes tick-borne disease

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Title: Study scale determines whether wildlife loss protects against or promotes tick-borne disease

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How does wildlife loss affect tick-borne disease risk? To test this question, Titcomb et al. [1] excluded large mammals that typically support large numbers of adult ticks from 1 hectare plots, and then quantified the density of questing adult ticks within exclosure versus control plots. *A priori*, one might expect reduced tick density within total exclosure plots, because adult ticks must take their final blood meal from an ungulate, hare, or carnivore (hereafter "large mammal") (Table 1), which were scarce to absent in exclosure plots (Titcomb et al. Figure S1). However, contrary to expectations, Titcomb et al. report higher density of questing adult ticks of two species (*Rhipicephalus pravus* and *R. praetextatus*) in exclosure plots compared to control plots, whereas the density of a third tick species (*R. pulchellus*) declined in exclosure plots. Here, we examine three possible explanations for this counterintuitive result, expanding on the interpretation offered by Titcomb et al. We submit that high densities of questing adult ticks in exclosure plots indicate that the tick population there is failing, not flourishing. This pattern is maintained through time because small mammals import ticks from outside the plot. Therefore, this pattern would be expected to reverse in a larger plot.

Given that all three tick species require large mammals to complete their life cycles [2,3, Titcomb et al. Figure S1, Table 1], Titcomb et al.'s results beg the question: why did the density of two tick species more than double in exclosure plots? Where did all those ticks come from? One explanation is that these ticks hatched before experimental treatments were implemented. Rand et al. [4] demonstrate that loss of large mammals that serve as final hosts for ticks can lead to an initial increase in questing tick density, followed by a crash in the tick population. This occurs because questing ticks that do not find a host continue to quest until they deplete their energy reserves and die [5]. However, the experimental plots used by Titcomb et al. were set up in 2008 [6]. Because experimental treatments had been maintained for >5 years before data were collected (and the reported pattern of increased tick density in exclosure plots remains to this day, Titcomb et al. pers. comm.), we consider it unlikely that adult ticks found in total exclosure plots hatched before experimental setup.

A second possible explanation is that questing adult ticks found in total exclosure plots hatched from eggs laid by gravid females that dropped off large mammals not excluded by the exclosure treatment. Although the total exclosure plots excluded or reduced the density of most large mammals on which ticks feed as adults, it is possible that a few carnivores (e.g., genets, mongooses) might have entered exclosure plots (Titcomb et al. Figure S1) and dropped gravid ticks. However, in a similar experiment (Kenya Long-term Exclosure Experiment; KLEE) in the same system, questing larval ticks were completely absent in plots that allowed carnivores and excluded large herbivores, but were common (~50 per 400m transect) in control plots that allowed all large mammals [7]. This pattern suggests that carnivores contributed only negligibly, if at all, to the tick population in exclosure plots.

Finally, a third explanation is that the ticks found in exclosure plots recruited there as larvae or as nymphs on rodents and shrews (hereafter "small mammals"), which are abundant [8] and small enough to freely cross plot fences. Previous studies have demonstrated fence-crossing behavior by small mammals [9], and suggested that this could explain increased tick densities inside large mammal exclosures [5,10,11]. G. Titcomb kindly provided data showing that density of questing adult *R. pravus/praetextatus* in the inner 25% of exclosure plots was more than double that in the outer 75% of exclosure plots (Figure 1A), but this pattern did not hold for *R. pulchellus*, nor did it hold in control plots (Titcomb, unpublished data). We consider this concentric increase in tick density from the edge of the exclosure to the center as convincing evidence that small mammals are crossing plot fences and moving larval and nymphal ticks with them. Although one might expect the opposite pattern (i.e., higher density of questing ticks near plot edges), the observed pattern likely resulted from the combination of tick import, tick export, and movement of ticks within plots (both independently and on small mammals). Perkins et al. [10] observed a similar pattern in small deer exclosures, and suggested that it resulted from tick "sharing"; small mammals whose home ranges overlap with the edge of exclosure plots dropped some of their ticks outside the plots, where they were picked up by large mammals. In contrast, small mammals whose home ranges are in the center of exclosure plots dropped all of their ticks in the plot center, where they continued to quest and could be detected in tick surveys. Hence, we consider the import of larval and nymphal ticks by small mammals to be the most plausible explanation for increased density of questing adult ticks in exclosure plots.

Regardless of whether ticks hatched in exclosure plots or were imported, the success rate of questing larval and nymphal *R. pravus/praetextatus* in exclosure plots might be especially high, because, in such plots, rodent density roughly doubles [8]. However, the success rate of questing adult ticks in exclosure plots should be quite low, as the large mammals from which ticks take their final blood meal are scarce to absent. As a result, adult ticks accumulate in total exclosure plots, where they continue to quest until they deplete their energy reserves and die, which might take months to years [4,12]. Compounding this, survival rates of questing ticks might be particularly high in exclosure plots compared to control plots, due to an abundance of vegetation [13]. Thus, for the two tick species that feed on small mammals as larvae and nymphs, exclosure plots are a sink. In contrast, the third tick species, *R. pulchellus,* does not feed on small mammals at any stage of its life cycle [2,3, Titcomb et al. Figure S1, Table 1]. This species declined in total exclosure plots relative to control plots, indicating that either it cannot mature in exclosure plots due to absence of large mammal hosts, or it cannot recruit into exclosure plots because it is not imported by small mammals.

Critically, if tick importation by small mammals explains the high density of questing adult ticks in exclosure plots, then this pattern is scale-dependent. Many ticks might recruit into a 1 hectare plot because the ratio of edge:interior habitat is high. In contrast, the center of a larger plot (e.g., 10 hectares) should be free of ticks (Figure 1B), because ticks cannot recruit there from outside the plot. Though such a large-scale study would be logistically challenging, it could reveal the effect of wildlife loss on ticks at a large scale; since large mammals are a required component of the tick life cycle (Table 1), reducing their density should negatively affect tick populations. In support of our assertion that Titcomb et al.'s results would reverse at a larger scale, in a similar experiment, the density of questing adult *R. praetextatus* did not differ between 4 hectare plots that allowed vs. excluded large wildlife [7]. Presumably, even fewer adult ticks would be found in an even larger exclosure plot. Indeed, Perkins et al. [10] found that compared to control areas, tick density increased in deer exclosures less than 2.5 hectares, but decreased in deer exclosures greater than 2.5 hectares. Although the studies included in this meta-analysis occurred in a different system (deer and their ticks in North America), the results should be expected to apply to any system in which larval and/or nymphal ticks take blood meals from small mammals and adult ticks rely on large mammals as hosts. However, the inflection point of 2.5 hectares would be expected to vary with study system, tick species, small mammal home range, environmental conditions, etc. [5].

We stress that Titcomb et al.'s results are valid at the scale at which they were measured; in a small plot, large mammals pick up ticks, thereby decreasing questing tick density (Figure 2A). Therefore, wildlife extirpation on local scales (such as might occur near human dwellings) should increase questing tick density [10] and potentially tick-borne disease risk for humans. However, at larger scales, Titcomb et al.'s results should reverse; large mammals produce ticks, thereby increasing questing tick density (Figure 2B). Therefore, wildlife extirpation on global scales should decrease questing tick density and tick-borne disease risk for humans. Although Titcomb et al. suggest that "wildlife loss can contribute to an increased tick-borne disease risk that may be mitigated by conservation," wildlife loss at larger scales is likely to have the opposite effect. We conclude that when examining the effects of biodiversity loss on infectious disease risk, researchers should carefully consider whether their results might reverse with scale.

Ethics

This work did not involve human or animal subjects.

Data accessibility

This article has no additional data.

Authors' contributions

J.C.B. developed the idea for the manuscript based on prior work by S.E.P. J.C.B. drafted the manuscript. J.C.B. and S.E.P. edited the manuscript and gave final approval for publication.

Competing interests

We declare we have no competing interests.

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164 **Table 1.** Hosts used by each tick species at each life stage. Reproduced from Titcomb et al.

165 Figure S1.

Tick species	**Life stage**	**Hosts**
R. pravus	Larva and nymph	Rodents Elephant shrews Hares Small carnivores
	Adult	Variety of ungulates Hares Carnivores
R. praetextatus	Larva and nymph	Rodents
	Adult	Carnivores Some ungulates Hares
R. pulchellus	Larva and nymph	Variety of ungulates Hares Carnivores
	Adult	Variety of ungulates Carnivores

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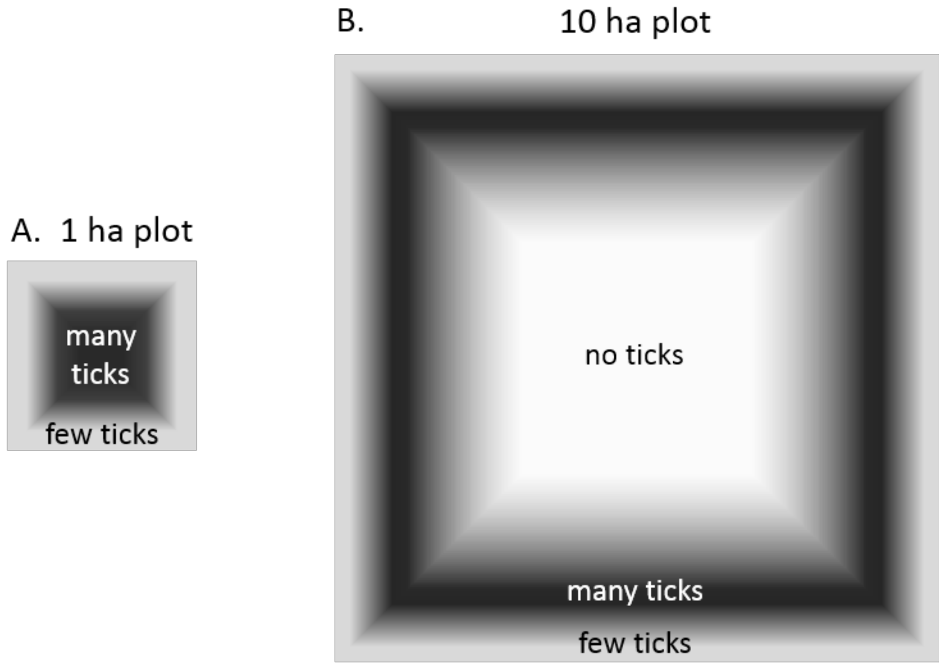
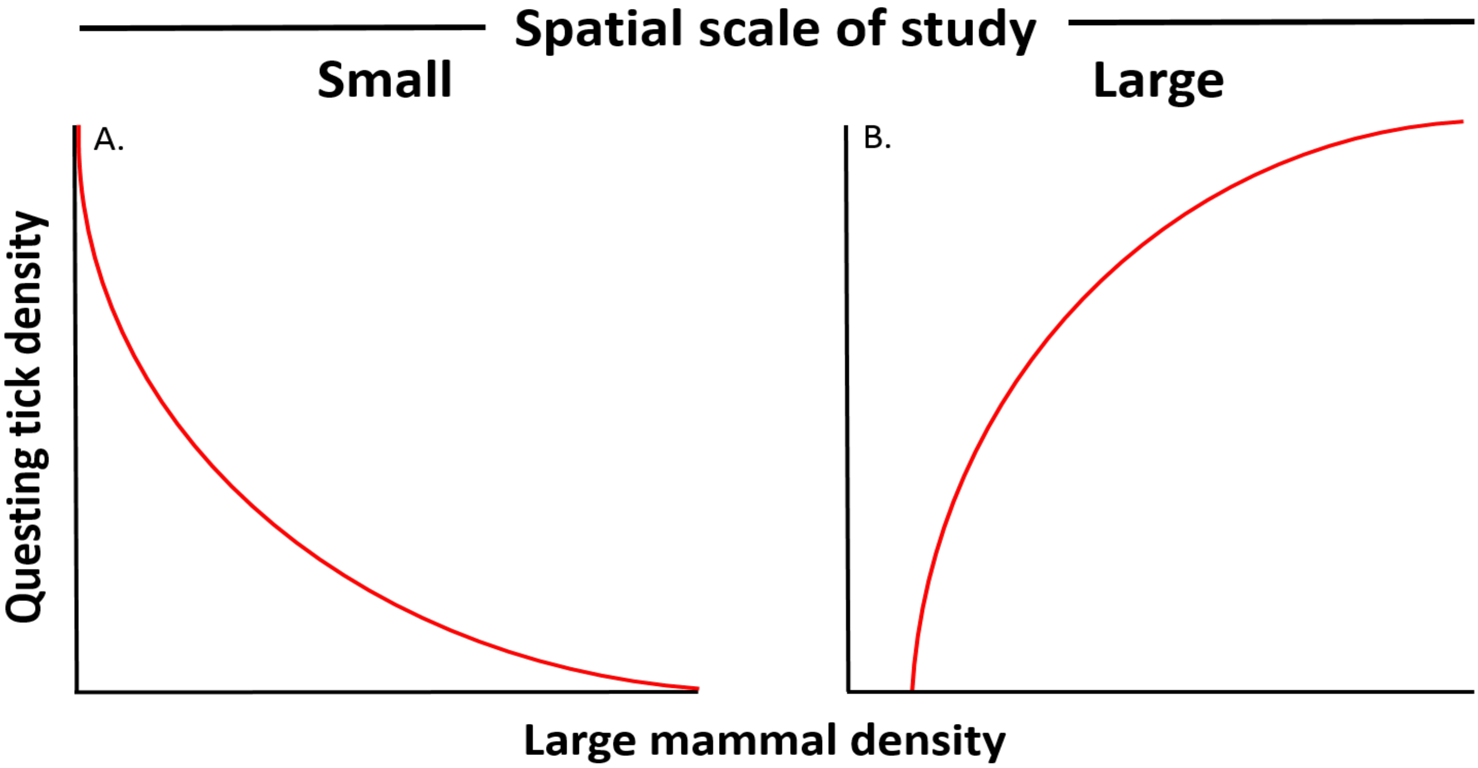
Figure 1. Conceptual figure showing the observed gradient in tick density in exclosure plots (A), which is likely due to tick "sharing," and the gradient we hypothesize would be found in a larger exclosure plot (B).

Figure 2. Conceptual figure showing that in a small-scale study (A), loss of large mammals increases questing tick density, as detected by Titcomb et al. [1]. However, in a study of larger spatial scale (B), loss of large mammals would be expected to reduce questing tick density, as ticks require large mammals to complete their life cycles. Non-linearities result from ticks distributing themselves among available large mammal hosts.


A. 1 ha plot
many ticks
few ticks
B.
10 ha plot
no ticks
many ticks
few ticks


Spatial scale of study
Small
Large
A.
B.
Questing tick density
Large mammal density